

## MEASUREMENT OF SPATIAL AUTOCORRELATION OF VEGETATION IN MOUNTAIN MEADOWS OF THE SIERRA NEVADA, CALIFORNIA AND WESTERN NEVADA

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### ABSTRACT

The presence of autocorrelation invalidates all standard statistical tests unless special corrections are made. Because of this, it is important to know the degree of spatial autocorrelation in order to know how to sample. Mountain meadows were sampled to determine spatial autocorrelation of vegetation at the plant community level. A total of 40 meadows were sampled in the eastern Sierra Nevada, California. At each meadow a dominant plant community was selected for sampling. Sampling consisted of placing 10 × 10 cm quadrats at 1-m intervals on a 20-m transect and recording the presence for all vascular plant species rooted in the quadrats. Sites varied in plant species composition and number of species present. For each plot, ordination analysis in the form of reciprocal averaging was used to derive positions for each quadrat on axis 1. The scores from axis 1 were analyzed by semivariance to obtain the spatial dependence of the quadrats. Overall, three semivariance patterns were seen; A) plant communities that were autocorrelated at distances of less than one meter; B) communities that were autocorrelated between 1 m and 15 m; C) communities that were autocorrelated at distances greater than 20 m. Results indicate that for semivariogram type B, on average, sites were autocorrelated to a distance of 3.6 m, meaning that quadrats separated by greater than 3.6 m were independent. Beta diversity was significantly ( $P < 0.05$ ) lower for semivariance type C than for either semivariance types A or B. These results are useful for determining spacing of sample points in mountain meadows to ensure spatial and statistical independence for presence/absence data.

Key Words: Beta diversity, meadow, sampling, spatial autocorrelation, vegetation.

One of the general patterns in ecology is that, on average, sites that are closer will be more similar (Fortin 1999). This is known as positive spatial autocorrelation (Mistral et al. 2000). The presence of autocorrelation invalidates all standard statistical tests unless special corrections are made (e.g., Dale et al. 1991). Because of this, it is important to know the degree of spatial autocorrelation in order to know how to sample. In this study, mountain meadows in the eastern Sierra Nevada, California were sampled to estimate the amount of autocorrelation within plant community types.

Methods for analyzing spatial autocorrelation in ecology have commonly been for univariate data (Fortin 1999). Such methods have been used, with single-variate indices such as Moran's  $I$  or Geary's  $c$ , on individual variates such as fruit production (Koenig and Knops 1998), plant height and diameter (Kuuluvainen et al. 1998), flower and vegetative characters (Chung and Noguchi 1998) and gene frequencies (Sokal et al. 1998). However, communities comprise many species, and are hence multi-variate. To examine the spatial pattern of gradients, workers such as Palmer (1988), Jonsson and Moen (1998), Ohlson

and Økland (1998), Meisel and Turner (1998), and Wagner (2003) summarized the whole community into ordination scores, and analyzed them by semivariance. This approach examines spatial variation in the major gradients, using only that fraction of the variation in species composition that is captured in the ordination.

Our aim is to document the spatial pattern for Sierra Nevada mountain meadow communities. We sampled with a fixed quadrat size (10 × 10 cm) using quadrats at 1-m intervals along a transect of 20 m length. The size of the quadrat from which species associations are calculated, as well as the length of transects may influence the detected association pattern (e.g., Ver Hoef et al. 1989). With very long transects, covering multiple habitat types and communities, environmental gradients will be captured (Rydgren et al. 2003). Such gradients are likely to occur as a result of environmental variation rather than as a cause of species interactions within specific plant communities. At the opposite end, with very short transects, stochastic effects, due to few individuals, may restrict the ability to detect significant spatial patterns among species (Jonsson and Moen 1998) within communities. The focus of

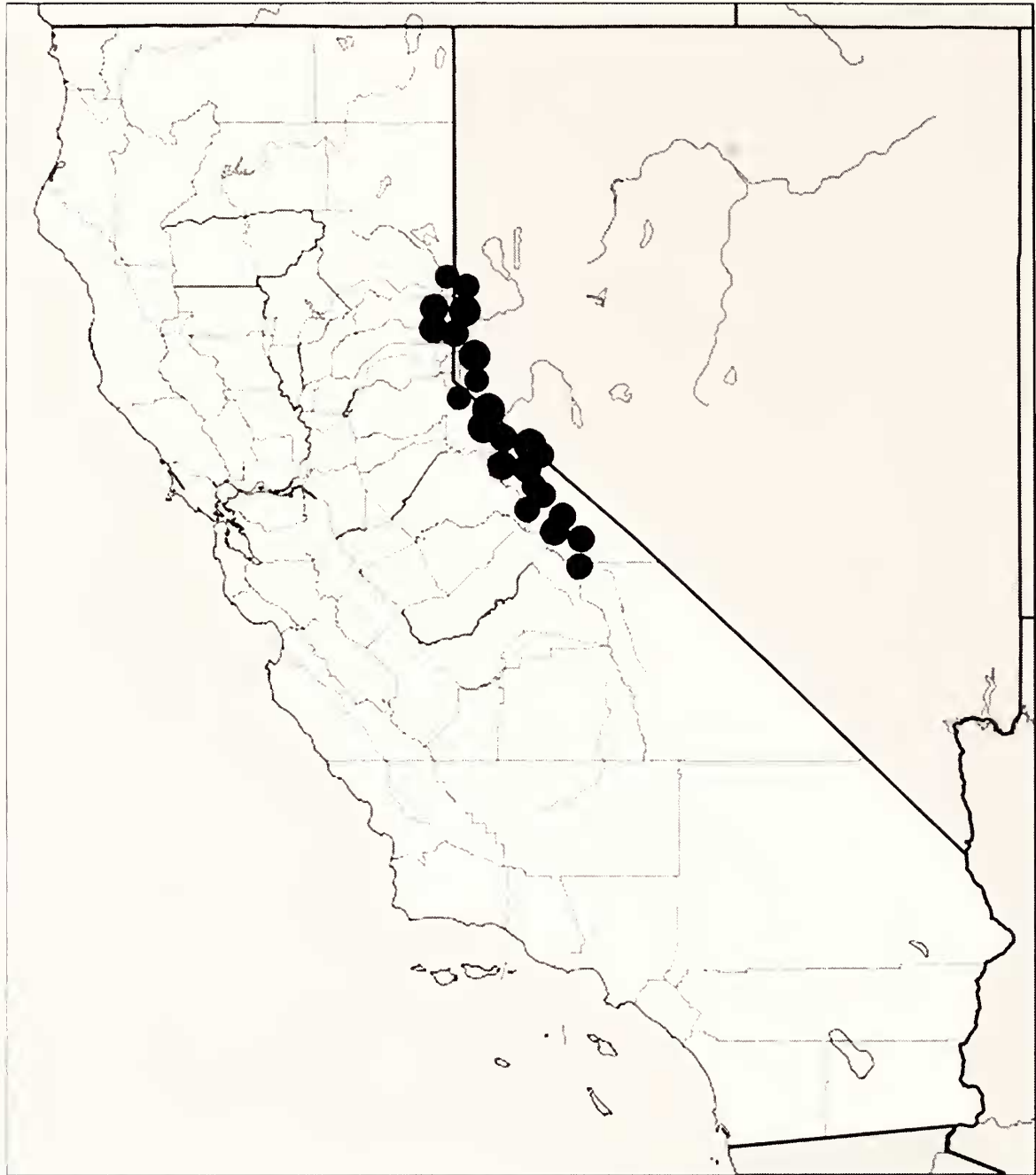


FIG. 1. Location of study sites in Sierra Nevada mountain range, California and eastern Nevada.

this paper is at intermediate scales, e.g., at the plant community level, where patterns in species associations and beta-diversity relate to the intrinsic patch sizes present within the plant community being sampled.

## METHODS

### Study Sites

Forty meadow sites were sampled in the eastern Sierra Nevada of California and Nevada at latitudes between  $38^{\circ}$  and  $40^{\circ}$  (see Fig. 1). All sites were located on National Forest lands. Livestock grazing had occurred on all sites since the 1860's and the sites are generally representative of the history of livestock grazing use in the Sierra Nevada. Sampling occurred between June of 1994 and August of 1996. Elevation of sites ranged from 7100 to 9600 feet. Depth to water table varied from 0 (at the surface) to 50 cm in mid-summer. All sites were classified as wet or moist meadow types using the USDA Forest

Service classification for Sierra meadows (Weixelman et al. 1996) and the dominant soil taxon was Typic Cryaquoll (Soil Survey Staff 1998). Species composition generally consisted of sedges, rushes, and forbs. Dominant species included Nebraska sedge (*Carex nebrascensis* Dewey), blister sedge (*Carex vesicaria* L.), western aster (*Aster occidentalis* Nutt.), Kentucky bluegrass (*Poa pratensis* L.), and yarrow (*Achillea millefolium* L.). At each site, a transect line 20 m in length was randomly located within a homogenous plant community and  $10 \times 10$  cm quadrats were placed at 1 m intervals along the transect for a total of 20 quadrats on each transect. Previous studies using presence absence methods in mountain meadows have used a  $10 \times 10$  cm quadrat size for sampling (Mistral et al. 2000; Moseley et al. 1986, 1989; Weixelman et al. 1996; USDA Forest Service 2008). The vegetation data consisted of presence/absence for each vascular plant species rooted in the  $10 \times 10$  cm quadrat. Plant nomenclature used in this paper conforms to Hickman (1993).



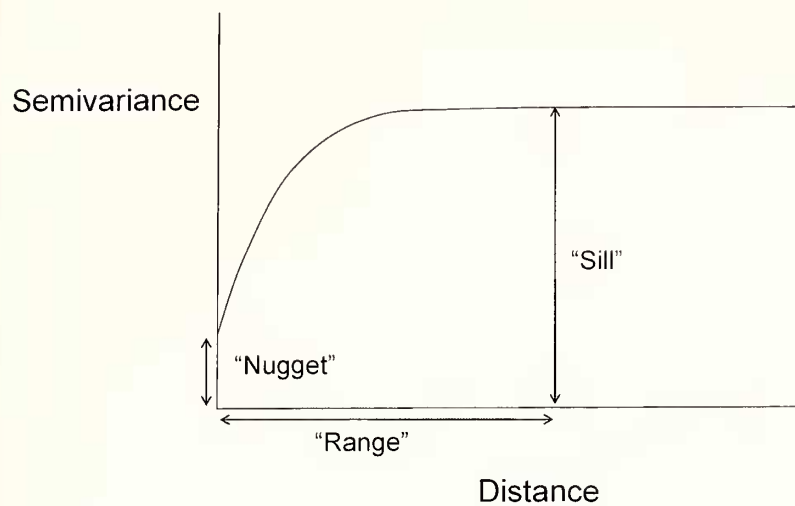


FIG. 2. Theoretical interpretation of a semivariogram with an asymptotical model showing the proportion of variance found at increasing distances of paired samples. The 'sill' is the variance around the average value of the variable. The 'range' is the maximum distance at which samples show spatial dependence, the 'nugget' is the variance found at a scale finer than the smallest sampling scale.

### Statistical Analysis

Species presence/absence data for each quadrat on a transect line was analyzed using reciprocal averaging (RA), an ordination program. RA is an indirect ordination technique which extracts gradients present in the species composition data assuming a unimodal relationship between the species abundance and the gradients (Hill 1973). To obtain a regionalized variable reflecting species composition, we used the ordination scores from reciprocal averaging (RA). RA then calculated scores on axis 1 for each quadrat. If the species composition in neighboring quadrats is similar, the ordination should place these quadrats close to each other in ordination space. However, if the species composition is unrelated to the spatial location of the quadrats, samples close to each other in ordination space may be considered randomly located in geographical space. Each site was analyzed for spatial independence using the data from the 20 quadrats. The ordination analyses were performed with the package PC-ORD version 3.0 (McCune and Mefford 1997).

Scores for each quadrat on axis 1 of RA were then analyzed by semivariogram (Robertson 1987) to examine the distance at which quadrats were autocorrelated within transects. Semivariograms are plots of the spatial dissimilarity (measured by semivariance) between points separated by known distances, plotted against those distances. Normally, points in close proximity are more similar than points farther apart, so that semivariance among points increases with distance until a maximum semivariance, called the sill, is reached (see Fig. 2). The distance at which the semivariance stops increasing is called the range, and the point where the semivariance begins (distance equals zero) is called the nugget.

Samples separated by distances closer than the range are statistically dependent, while those separated by distances greater than the range, are not, because at distances greater than the range the semivariance equals the sample variance, implying zero spatial correlation (Trangmar et al. 1985).

Using the geostatistical package GS+, we calculated semivariograms of the quadrats using the axis 1 scores from ordination. Semivariances were calculated up to within 10 pairs of the maximum distance between all points (i.e., 20 m). For transects that exhibited spatial autocorrelation, semivariogram models for range, nugget, and sill were fit using a non-linear least squares technique (Robertson 1987). These models included linear with a sill, spherical, exponential, and Gaussian curves. We chose the best fitting of these four curves based on the best fit of the residuals about the curve, particularly at the sill and nugget ends of the curve. If a transect exhibited zero autocorrelation, the sample variance was used for sill and nugget variances and zero was used for the range. If a transect exhibited spatial autocorrelation with no sill it was considered to have a nonstationary mean (Trangmar et al. 1985). In this case, the samples were dependent out to the maximum distance of the transects, in this case 20 m. Because mountain meadows are made up of a patchwork of a number of plant communities, the size of each community is sometimes less than 20 m and sometimes greater than 20 m. Based on the author's experience, at distances much greater than 20 to 30 m, changes in environment, including changes in hydrology, become significant and changes in plant composition are more likely due to environmental gradients.

### Beta Diversity

Robert H. Whittaker (1960) defined beta diversity as the variation in species composition among sites in a geographic area. In our case, this is the variation in species composition among quadrats along the transect line. Whittaker (1960) established a straightforward measure of beta diversity, which will here be called  $\beta_w$ :

$$\beta_w = (s/a) - 1$$

where  $\beta_w$  = beta diversity,  $s$  = total number of species occurring on the transect, and  $a$  = average number of species occurring in the quadrats. The measure  $\beta_w$  is easy to calculate and explicitly relates the components of diversity  $a$  and  $\beta$ , to overall diversity,  $s$ .

### Statistical Tests

All statistical tests were performed using SPSS version 9.0 (SPSS 1998). Tests of significance

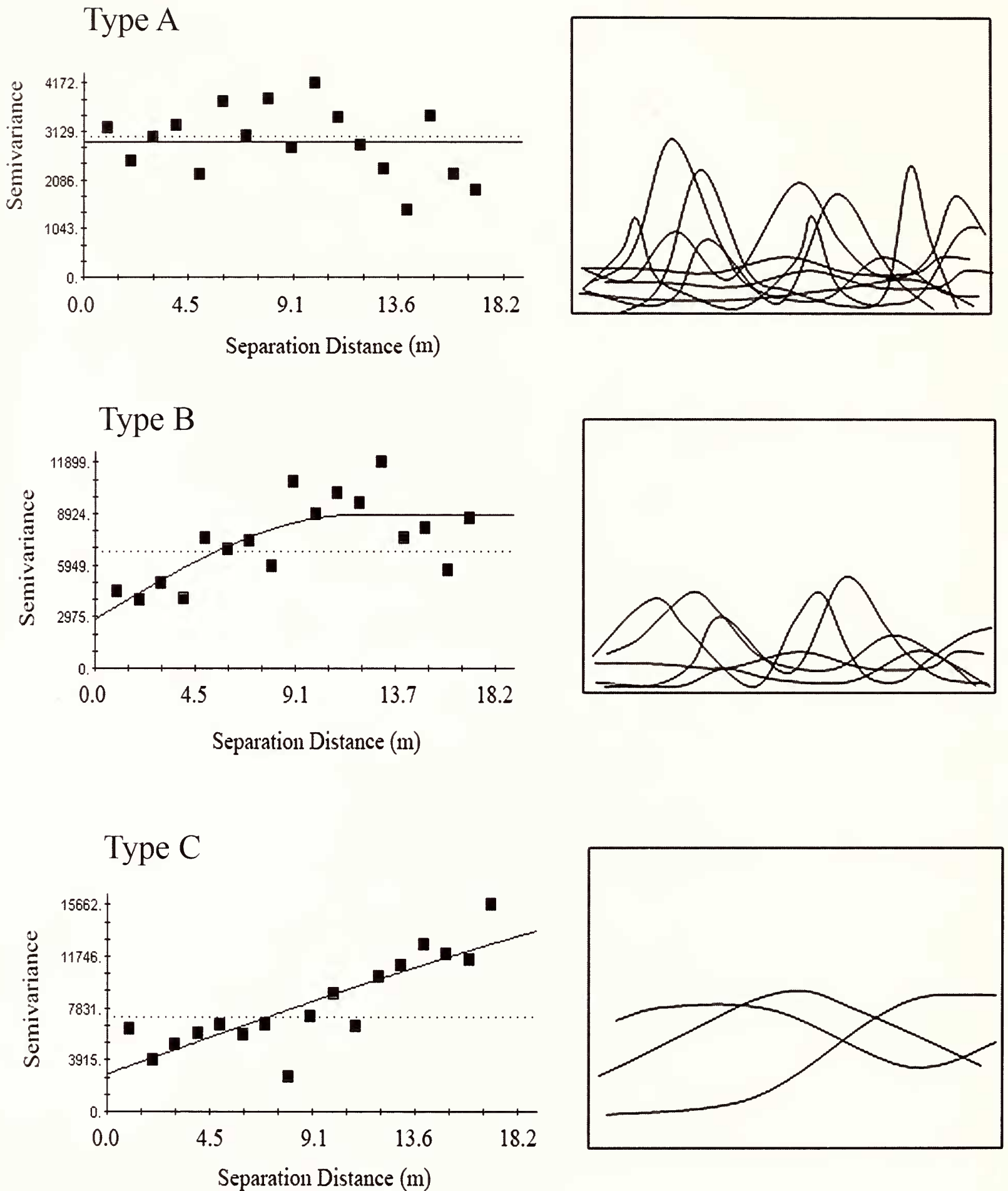


FIG. 3. Semivariograms of data taken from three individual sites to illustrate three types of spatial pattern. The dashed lines denote the semivariance around the average value. Type A: communities that showed no clear spatial pattern, i.e., autocorrelation of less than 1 m; type B: meadow communities with a clear range and sill; and type C: meadow communities with an increasing semivariance beyond 20 m separation, i.e., autocorrelation to distances beyond 20 m. Also shown are stylized diagrams illustrating species turnover (curved lines on the right) along a transect.



TABLE 1. MEAN AND STANDARD DEVIATION OF BETA DIVERSITY AND AVERAGE NUMBER OF SPECIES BY TYPE OF SEMIVARIOGRAM. Superscripts that are different within the same column represent a statistically significant difference ( $P < 0.05$ ).

| Type of semivariogram | Beta diversity    | Average number of species | Average elevation (m) |
|-----------------------|-------------------|---------------------------|-----------------------|
| A (n = 20)            |                   |                           |                       |
| Mean                  | 2.56 <sup>a</sup> | 11 <sup>a</sup>           | 2679 <sup>a</sup>     |
| SD                    | 1.28              | 6                         | 328                   |
| B (n = 13)            |                   |                           |                       |
| Mean                  | 2.59 <sup>a</sup> | 12 <sup>a</sup>           | 2686 <sup>a</sup>     |
| SD                    | 0.88              | 5                         | 208                   |
| C (n = 7)             |                   |                           |                       |
| Mean                  | 1.33 <sup>b</sup> | 7 <sup>b</sup>            | 2668 <sup>a</sup>     |
| SD                    | 0.92              | 2                         | 360                   |

were used to determine if differences existed in beta diversity and number of species on a site for classes of differing spatial pattern.

## RESULTS

Results of ordinating quadrat data followed by semivariance analysis showed three general spatial patterns of vegetation (see Fig. 3): Type A, B, and C. The semivariogram for type A communities was generally flat, with no range evident. Therefore, plant species in this type were autocorrelated at distances of less than 1 m, which was the smallest scale measured in this study. These sites were higher in beta diversity and contained many species. The semivariogram for type B communities exhibited a distinct range and sill between 1 m and 20 m. Sites in type B were positively autocorrelated to a distance of 3.6 m on average. The semivariogram for type C communities showed a continual rise with no sill or range visible. Quadrats in this type were positively autocorrelated at distances greater than 20 m.

In type A communities, species turnover as indicated by the  $\beta$ -diversity index was high (see Table 1) as was the average number of vascular plant species on the sites. In type B communities,  $\beta$ -diversity was also high. Sites in this type typically had high numbers of species with rapid turnover in composition along transects as indicated by the high  $\beta$ -diversity index for these sites. The semivariogram for type B showed a range at distances ranging from 3 m to 15 m (Fig. 3, type B). The average distance at which quadrats were autocorrelated in type B communities was 3.6 m. The  $\beta$ -diversity index averaged nearly the same as for type A (Table 1). The number of species for type B was also similar to type A. Type C plots had the lowest  $\beta$ -diversity of the three semivariance types (Table 1). In addi-

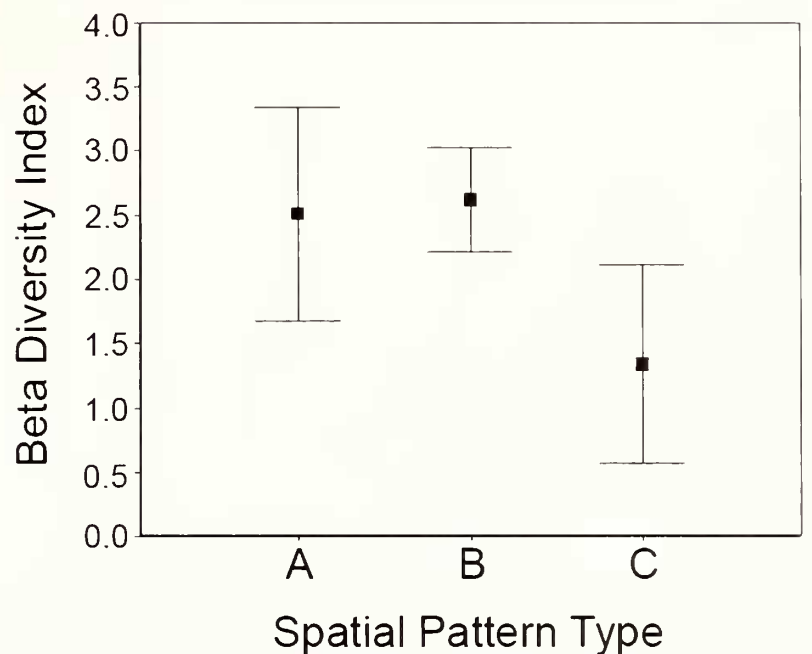


FIG. 4. Comparison of beta diversity among the three types of spatial pattern seen (A, B, and C), see text for explanation of types of spatial pattern. Error bars represent 95% confidence interval.

tion, type C had the lowest average number of species on each site. Significant differences ( $P < 0.05$ ) in  $\beta$ -diversity were found between type A and B as compared to type C communities.

## DISCUSSION

Spatial patterns of herbaceous species in meadows vary with environment, species ecological characteristics, species interactions, grazing, and ground disturbing activities. In this study, sites were located within a plant community in order to limit variation based on environmental factors. Therefore, results of this study are most applicable in situations where one is interested in spatial variation within meadow plant communities that typically occur in the Sierra Nevada.

The three types of plant community spatial patterns were different in their pattern of spatial autocorrelation (Fig. 3). In this study, plant community spatial patterns were positively autocorrelated according to the following rank distances: type A < type B < type C. Type C communities were typically homogeneous stands dominated by clonal graminoid species including sedges and/or rushes. These stands had fewer species than either type A or B. In contrast, type A and B communities were composed of many small forbs including species indicating disturbance as well as clonal graminoid species. Most species present were either obligate wetland (OBL), facultative wetland plant species (FACW) or facultative wetland species (FAC) using the U.S. Fish and Wildlife wetland rating system for plants (U.S. Fish and Wildlife Service 1988).

Robert H. Whittaker (1960) defined beta diversity as the variation in species composition among sites in a geographic area. In our case, this is the variation in species composition among

quadrats along the transect line. Using Whittaker's equation provides an index of the variation in number of species present in each quadrat along the transect line, in this case 20 m. For homogenous plant communities, such as clonal patches of sedges, the beta diversity was low. The 95% C.I. for beta diversity in type C ranged from 0.55 to 2.2. Plant communities in this group were typically clonal, rhizomatous sedge species and included Nebraska sedge (*Carex nebrascensis*), Blister sedge (*Carex vesicaria*), and analogue sedge (*Carex simulata* Mack.). Beta diversity in type A and B were higher due to more species and higher density of individual plants and ranged from 1.9 to 3.4 in type B and 2.2 to 3.1 in type A (95% C.I.). Type A and B communities were not different in beta diversity even though semivariance diagrams were different between the two groups. Type A communities did show a higher beta diversity for some plots but generally overlapped type B when the 95% C.I. was plotted (see Fig. 4). Type A communities were autocorrelated at distances of less than one meter, while type B communities were autocorrelated at an average distance of 3.6 m. Type A and B communities were composed of early successional forbs and a mix of graminoid species. Typical plant species present in type A and B communities included Kentucky bluegrass (*Poa pratensis*), western yarrow (*Achillea millefolium*), and western aster (*Aster occidentalis*). These types were representative of disturbance communities and meadow types with larger seasonal fluctuations in water table.

Significant differences ( $P < 0.05$ ) in  $\beta$ -diversity were found between type A and B as compared to type C communities. Thus, knowing the  $\beta$ -diversity of a plant community using the methods described here could potentially be used to determine which type of spatial pattern exists in a meadow community. Spatial pattern will depend both on the size of the quadrat being used and the distance separating the quadrats. Spatial pattern may also vary depending on soil moisture types, drier meadows would be expected to be different than wet meadows based on wider spacing of plants in drier meadows.

For practical considerations and sampling in the field, beta diversity can be used as a rough indicator of spatial autocorrelation in plant communities. When determining rooted frequency using the  $10 \times 10$  cm frame as in this study and 1 meter spacing along transect lines, a beta diversity value using the Whittaker index of less than about 2.2 would indicate, with high probability, a spatial autocorrelation distance greater than 20 m. While a beta diversity index of greater than 2.2 would indicate a spatial autocorrelation distance closer to that expected for semivariance types A and B. It is reasonable to expect the spatial

relationships of the plant community to vary in different environments, and some care must be taken when trying to extrapolate the results of this work.

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